



Road verges are important secondary habitats for grassland arthropods

Hardeep Kaur^{1,2} · Attila Torma¹ · Nikolett Gallé-Szpisjak² · Jelena Šeat^{1,3} · Gábor Lőrinczi¹ · Gábor Módra¹ · Róbert Gallé^{1,2}

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Abstract

Semi-natural linear landscape elements such as road verges, hedgerows and field margins are important in maintaining the connectivity between habitat fragments of highly modified landscapes. Preservation of habitat specialist fauna requires conservation of the remaining natural habitat patches and connectivity of fragments. Our study focuses on the spider, ant and true bug fauna and functional diversity (FD) of fragmented forest steppe patches, moderately grazed pastures and road verges embedded in a matrix of forest plantations in Hungary, Central Europe. We established total 30 sampling sites, 10 in each, the grassland component of forest-steppes (F), pastures (P) and road verges (R) near pine forests. We collected arthropods with pitfall and sweep-net techniques. We calculated FD and species composition of arthropods using linear mixed models. We observed higher species richness in road verges for spiders and ants. We also found higher FD values for spiders and different trait composition for all taxa in road verges when compared with forest steppes and pastures. Species composition suggests that road verges do not serve as habitat for several forest-steppe and grassland species, in spite of the fact that numerous specialist species were found in the road verges. We show that forest steppes have higher species richness of spiders than pastures, and there are differences in species assemblage composition of the two habitat types for all taxa. Our results indicate that road verges should be considered as an important refuge for grassland specialist arthropods, as road verges provide secondary linear habitats for many arthropod species, and we would suggest the maintenance of these grassy strips in order to preserve arthropod biodiversity.

Keywords Managed forest · Functional diversity · Secondary habitat · Forest steppe · Pasture · Road verge

Introduction

In fragmented agricultural landscapes of Europe, the availability of natural, semi-natural habitats has been highlighted as the limiting factor for the conservation of populations.

Preservation of habitat specialist fauna in fragmented habitats requires conservation of natural habitat patches and connectivity of fragments. Artificial linear landscape elements (LLEs) are landscape structures established for a special function such as transportation on roads and drainage by ditches, but they have a part covered by vegetation, which is not directly used for its original function, and may potentially constitute semi-natural habitats. It is shown that a significant proportion of native biota can survive in LLEs such as ditch banks (Torma et al. 2018) field margins and hedgerows (Ernoult et al. 2013; Gallé et al. 2018a; Haaland et al. 2011; Morandin and Kremen 2013), road and railway verges (Henneberg et al. 2017; Jakobsson et al. 2018; Noordijk et al. 2009). These LLEs are important in conserving various arthropods and other animals as they can decrease isolation effect of fragmented habitats (Dover et al. 2000; Hinsley and Bellamy 2000; MacDonald 2003; Hollmen et al. 2008) and also, they function as corridors

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✉ Hardeep Kaur
hardypabla@gmail.com

- ¹ Department of Ecology, University of Szeged, Közép fasor 52, Szeged 6726, Hungary
- ² MTA Centre for Ecological Research, Institute of Ecology and Botany, Lendület Landscape and Conservation Ecology, Vácrátót, Alkotmány u. 2-4., Vácrátót 2163, Hungary
- ³ HabiProt, Janka Čmelika 28a/25, 21000, Novi Sad, Serbia

and refuges for species within highly modified landscapes (Zanden et al. 2013). Road verges between patches, for example, proved to have importance in conserving grassland specialist fauna in Ireland (Fuller et al. 2013) and also Noordijk et al. (2009) showed that apart from indigenous species of ants, grasshoppers, spiders, ground beetles, bees and butterflies, road verges were able to save several threatened species of grasshoppers and bees in intensively used landscapes in the Netherlands. LLEs can help in increasing species movements across the fragment habitat (Gilbert-Nortan et al. 2010). Although, road verges in fragmented habitats usually undergo management activities like mowing and subsequently changing the composition of communities. Careful management and preservations of road-side verge can help to protect biota (Le Viol et al. 2008; Decler et al. 2015).

Forest-steppes are defined as an alternation of forest patches within steppe grasslands forming a mosaic-like structure (Erdős et al. 2014). An extensive forest-steppe belt has been developed in the Eurasian temperate zone under semi-humid to semi-arid climate, and it runs from the Pannonian lowland to China. The westernmost occurrence of forest-steppe is in the Hungarian Great Plain, where open forest patches are embedded in xeric grasslands (Erdős et al. 2018). Since grasslands are characterized by a higher temperature and lower humidity than forests, both habitat types have their own specialised fauna (Gallé et al. 2018b). Hungarian forest-steppes have lost more than 93% of their original areas during the past 200 years. The most important threatening factors of this habitat type and its high of conservation value invertebrate fauna are afforestation, overgrazing and desertification due to the drop of groundwater table and climate change (Molnár et al. 2012).

The majority of forest steppes in Hungary are altered by anthropogenic activities such as forest management to meet the growing forestry demands and to stabilize the sandy soil in open grasslands (Molnár et al. 2012). In addition to native deciduous forest plantations, exotic species like black locust (*Robinia pseudoacacia*) and scots pine (*Pinus sylvestris*) were introduced to the Great Hungarian Plain at the beginning of the seventeenth and at the end of the nineteenth century, respectively (Redei et al. 2008; Masón and Alía 2000). In this region, there also exists extensive sandy grasslands, that are regularly used for pasture and maintained by sheep or cattle grazing thus they are in a semi-natural form (Biró et al. 2013). Intensive management of these grasslands threatens biodiversity (Dengler et al. 2012). However, grasslands with sparse woody vegetation and are moderately grazed can maintain diverse species richness (Kőrösi et al. 2011; Gallé et al. 2017). Overgrazing of the grasslands on the other hand leads to structural simplification of the habitat, and thus have negative effect on arthropod fauna (Horváth et al. 2009; Habel et al. 2013).

Arthropods represent a widely used indicator group in conservation studies, as they are highly diverse and present in almost every terrestrial and aquatic habitat. They interact with various other groups and are important mediators of ecosystem. In our study, we focused on three arthropod taxa, spiders (Araneae), true bugs (Heteroptera) and ants (Hymenoptera: Formicidae). Spiders are among the most abundant invertebrate predators, that play a decisive role in the regulation of other invertebrate assemblages (Clarke and Grant 1968; Moulder and Reichle 1972; Weeks and Holtzer 2000). The diversity of spiders is affected by a number of environmental factors that directly control their microhabitat requirements (Ziesche and Roth 2008). True bugs are the largest and most diverse group of hemimetabolous insects. They comprise phytophagous, zoophagous and omnivorous feeders (Fauvel 1999). Their presence in particular habitat reflects habitat condition primarily determined host plants for phytophagous and omnivorous species, whereas vegetation structure and prey availability specify the suitable habitat for zoophagous species (Gallé et al. 2010). Ants are one of the most ecologically important animal groups in many terrestrial ecosystems. They are highly diverse, abundant, sensitive to change in the environment and can provide cost effective and efficient data compared to other invertebrate groups (Andersen and Majer 2004). They play complex role as predators, herbivores, seed-dispersal agents and soil engineers (Hölldobler and Wilson 1990). Any change in their micro or macrohabitat such as shading effect, soil type or vegetation cover directly affect their community structure in nature (Andersen et al. 2002). Ants respond quickly to changes in their habitat such as the clearing of forests (Majer et al. 1997), road construction (Lassau and Hochuli 2004), anthropogenic disturbances or agricultural practices (Evans et al. 2011) hence, are reliable bioindicators.

Traditionally, species richness has been used as a diversity measure of ecosystems, neglecting the functional diversity (FD) approach. However, change in the FD of species corresponds to all the functions provided by these species in an ecosystem, thereby being able to predict ecosystem processes, dynamics and stability (Petchev and Gaston 2006). Therefore, FD provides a more accurate picture of the change of ecosystems due to changes in habitats (Díaz and Cabido 2001).

In this research, we aim to study the species richness and FD of the arthropod fauna of forest-steppe patches, pastures, and road verges within exotic forest plantations. We focus on addressing the following questions: (1) Do linear grassy strips along road verges have a role in maintaining the steppe species of arthropods? (2) Are the forest-steppe grasslands different from pastures in terms of arthropod species composition and FD (functional trait composition, RaoQ diversity)? (3) Is there any difference in the species composition between the studied habitat types?

Materials and methods

Study region

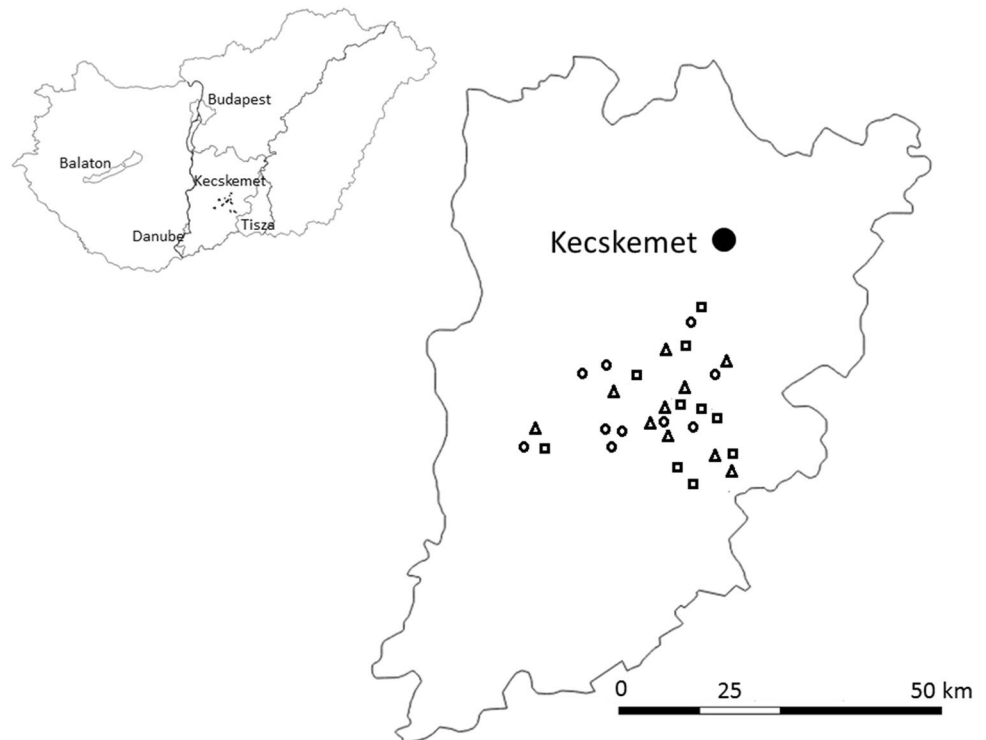
Our study was conducted in the southern part of Hungary, in the Danube–Tisza Interfluvium (47.1625°N, 19.5033°E, elevation approximately 100 m asl, Fig. 1). The climate is continental with some Mediterranean influence (Borhidi 1993). Mean annual precipitation is 500–550 mm, which decreases from NW to SE, and the mean annual temperature is ca. 10 °C with a semi-arid period in late summer (Fekete et al. 2002). The soil is a sandy silt and loess rich soil, which were originally formed through regular flooding of the Danube River. The main natural habitat type of the study region is a forest-steppe. The typical vegetation of grassland component of forest-steppe consists of drought tolerant tall grasses, mainly *Festuca vaginata* and *Stipa borysthena* coupled with few dicots such as *Alkanna tinctoria*, *Dianthus serotinus*, *Fumana procumbens*, *Iris arenaria* and *Onosma arenaria* (Molnár et al. 2012; Erdős et al. 2015). Road verges consist of generalist plant species along with some steppe grassland species such as *F. vaginata*, *S. borysthena* and *A. tinctoria* (personal observation).

Study sites and sampling design

Ten sites in each habitat, the grassland component of forest-steppes (F), pastures (P) and road verges (R) near

pine forests were assigned for sampling, respectively. We excluded potential sampling sites with significant cover of invasive plant species like *Asclepias syriaca*, *R. pseudoacacia* and *Ailanthus altissima*. All study sites were in the range of approximately 50 km and were minimum 1 km apart and around four villages (Zsana, n = 5; Imrehegy, n = 3; Pirtó, n = 7; Tázlár, n = 15). In each site, four pitfall traps were arranged in a transect at 5 m intervals to sample ground-dwelling arthropods. Traps were 500 ml white plastic cups, 8.5 cm in diameter, and they were provided with a metal roof and plastic funnel to prevent the preservative from dilution by rain or entry of vertebrates (Császár et al. 2018). We used 50/50 ethylene glycol/water mixture in pitfall traps as a preservative. In addition to pitfall traps, we also used sweep net technique to sample vegetation dwelling arthropods. At each site, we collected 5e samples, each comprised of 25 sweeps along ca. 20 m transect. Pitfall traps were open twice between 6th and 16th June and between 11th and 26th September 2017, respectively. Sweep net sampling was done on the 16th of June and the 26th of September. Data were pooled per site for further analysis. We identified the collected invertebrates using the keys of Nentwig et al. (2019) for spiders, and key of Czechowski et al. (2012) for ants. To identify true bugs, we used various keys (Wagner and Weber 1964; Schuh et al. 1995; Matocq 2004; Rabitsch and Deckert 2007). Voucher specimens were stored in the collection of the Department of Ecology, University of Szeged, Hungary.

Fig. 1 Map of the study region. Road verges, forest-steppe, and pastures are represented by square, circle and triangle, respectively, in the Danube–Tisza Interfluvium



Data analysis

We used three ecological traits to characterize the sampled arthropod species: moisture preference, shading tolerance and dispersal ability (Table 1). Species were assigned with a specific value from 0 to maximum 5 for each trait. If a given species fell under more than one category, then an averaged value was assigned. Generalist species or species with no data available in any trait category were excluded from further calculations. Species were considered as generalist if they fell under more than the half of the categories. All trait values were ranged between 0 and 1 to account for the different number of categories. We did not perform any statistical analysis on the dispersal ability of ants because the overwhelming majority of the collected species disperse only by nuptial flight.

We calculated the single trait FD measure, community weighted mean (CWM) for all traits of the three arthropod groups, and we used the multivariate RaoQ index to characterize FD of our sampling sites with the FD package in R (Laliberté et al. 2014).

We used linear mixed models to determine the effect of habitat type as fixed effect (i.e., F, P or R) and villages as a random effect on species richness and FD indices. We used negative binomial and Poisson error term for species richness after checking for overdispersion of data for spiders, true bugs and ants respectively. We used Gaussian error term for CWM and RaoQ indices. Pairwise comparisons were carried out using the “relevel” function in R.

We performed analysis of similarities (ANOSIM) based on Bray–Curtis dissimilarity matrices with 10,000 permutations to test the multivariate differences among the arthropod assemblages in the three habitats types using “anosim” function of the vegan package in R (Oksanen et al. 2015). We visualized this data set with non-metric multidimensional scaling based on the Hellinger transformation (Legendre and Gallagher 2001) using vegan package 2.4-6. A maximum number of 20 random starts were used to search for a stable solution to fit into the two-dimensional plot. We also performed an indicator value analysis to identify the characteristic species in forest steppe, pastures and road verges (IndVal; Dufrene and Legendre 1997) with the ‘labdsv’ package (Roberts 2012).

Results

We collected a total of 6983 spider individuals (out of which 1598 were adults and could be identified to species level and for all others that follow), 5537 adult true bugs and 16,425 adult ants from 114, 147 and 27 species, respectively. Altogether, we found 72 spider, 85 true bug and 19 ant species in forest steppe grasslands; 51 spider, 87 true bug and 16 ant species in pastures; and 75 spider, 92 true bug and 22 ant species in road verges. Among spiders, *Oxyopes heterophthalmus* (Latreille, 1804), *Tibellus macellus* (Simon, 1875) and *Zelotes longipes* (L. Koch, 1866) were the most common, comprising approximately 35% of all individuals. True bugs were largely represented by the rhopalids, and

Table 1 Functional diversity traits for spiders, true bugs and ants

Spiders	True bugs	Ants
Moisture preference		
Very dry: 1	Very dry: 1	Xerothermic: 1
Dry: 2	Dry: 2	Mesothermic and xerothermic: 2
Semi humid: 3	Semi humid: 3	Mesothermic: 3 (Czechowski et al. 2012)
Humid: 4	Humid: 4	
Very humid: 5 (Buchar and Ruzicka 2002)	Very humid: 5 (Wachmann et al. 2012)	
Shading tolerance		
Open: 1	Open: 1	Open: 1
Semi open: 2	Semi open: 2	Semi open: 2
Partly shaded: 3	Partly shaded: 3	Shaded: 3 (Czechowski et al. 2012)
Shaded: 4 (Buchar and Ruzicka 2002)	Shaded: 4 (Wachmann et al. 2012)	
Dispersal		
Not included in lists: 1	Shortened-winged: 1	Excluded
Members of the same family balloon: 2	Predominantly shortened-winged: 2	
Members of the same genus balloon: 3	Equally shortened-winged and macropterous species (including sexual dimorphism): 3	
Species known balloon: 4 (Bell et al. 2005; Blandenier 2009)	Predominantly macropterous species: 4	
	Macropterous species: 5 (Wachmann et al. 2012)	

Rhopalus parumpunctatus (Schiling, 1829) and *Chorosoma gracile* (Josifov, 1968) were the most abundant species, together more than 27% of the total catch. The most abundant ant species were *Plagiolepis taurica* (Santschi, 1920), *Lasius psammophilus* (Seifert, 1992) and *Tetramorium cf. caespitum* (Linnaeus, 1758), accounting for approximately 70% of all individuals.

Linear stripes along the road verges had higher species richness of spiders and ants than pastures, however, true bug species richness was similar in all three habitats (Table 2). Road verges had higher spider FD (RaoQ) than the other two habitat types (Table 2). We also found higher moisture preference values in the road verges than in the other two

habitat types for all arthropods, furthermore, CWM shading tolerance was also higher in the road verges for spiders and true bugs than in forest-steppes and pastures (Table 2). The highest dispersal CWM values were also found in road verges for true bugs, however, we did not find any significant difference in the dispersal ability of spiders.

We found significant differences in the species composition of spiders (ANOSIM: $R=0.282$, $p<0.001$), true bugs (ANOSIM: $R=0.4774$, $p<0.001$), and ants (ANOSIM: $R=0.211$, $p<0.001$) between habitats. Road verges and pastures were the most distinct habitat pair, with little overlap between them according to the NMDS scatterplot (Fig. 2). Significant indicator species in all three habitats were found

Table 2 Summary statistics of linear mix models for species richness and functional diversity of spiders, true bugs and ants in forest steppes (F), pastures (P) and road verges (R)

Species richness ^{a,b}	RaoQ ^c	CWM moisture ^c	CWM shading ^c	CWM dispersal ^c
Spiders				
F–P				
-0.305 ± 0.231	-0.136 ± 0.327	0.002 ± 0.023	-0.03 ± 0.049	0.041 ± 0.056
-2.573^* (25)	-0.819 (26.98)	0.186 (26.56)	-1.206 (27)	1.377 (27)
F–R				
0.0295 ± 0.217	0.364 ± 0.329	0.030 ± 0.256	0.097 ± 0.049	0.058 ± 0.056
0.264 (25)	2.166* (26.6)	2.295* (26.8)	3.84*** (27)	1.945 (27)
P–R				
0.334 ± 0.211	0.50 ± 0.313	0.027 ± 0.023	0.128 ± 0.049	0.016 ± 0.056
3.095** (25)	3.117** (23.6)	2.266* (23.9)	5.04*** (27)	0.568 (27)
True bugs				
F–P				
0.047 ± 0.231	0.255 ± 0.341	-0.053 ± 0.058	-0.022 ± 0.05	-0.087 ± 0.066
0.404 (25)	1.438 (26.41)	-1.772 (27)	-0.796 (27)	-2.54^{**} (26)
F–R				
-0.060 ± 0.235	-0.028 ± 0.352	0.092 ± 0.025	0.075 ± 0.05	0.115 ± 0.066
-0.505 (25)	-0.158 (26.75)	3.045** (27)	2.626** (27)	3.355** (25.5)
P–R				
-0.108 ± 0.233	-0.284 ± 0.327	0.145 ± 0.025	0.097 ± 0.05	0.203 ± 0.066
-0.909 (25)	-1.702 (24.17)	4.817*** (27)	3.422** (27)	5.903*** (25)
Ants				
F–P				
-0.195 ± 0.305	-0.264 ± 0.666	-0.008 ± 0.147	-0.059 ± 0.115	
-1.247 (26)	-0.779 (26.93)	-0.118 (26.91)	-1.000 (25.58)	
F–R				
0.279 ± 0.272	0.296 ± 0.672	0.234 ± 0.147	-0.036 ± 0.115	
1.999* (26)	0.865 (26.96)	3.019* (26.98)	0.618 (24.79)	
P–R				
0.475 ± 0.290	0.561 ± 0.635	0.243 ± 0.139	0.022 ± 0.115	
3.209*** (26)	1.731 (23.48)	3.398** (23.7)	0.382 (24.8)	

Model estimate \pm 95% CI; z/t values are given. Significances marked with stars and significant results are marked in bolds. Degree of freedom is shown in brackets

Significance levels: * <0.05 , ** <0.01 , *** <0.001

^aLinear mix models with negative binomial error term

^bLinear mix models with Poisson error term

^cRegression model with Gaussian error term

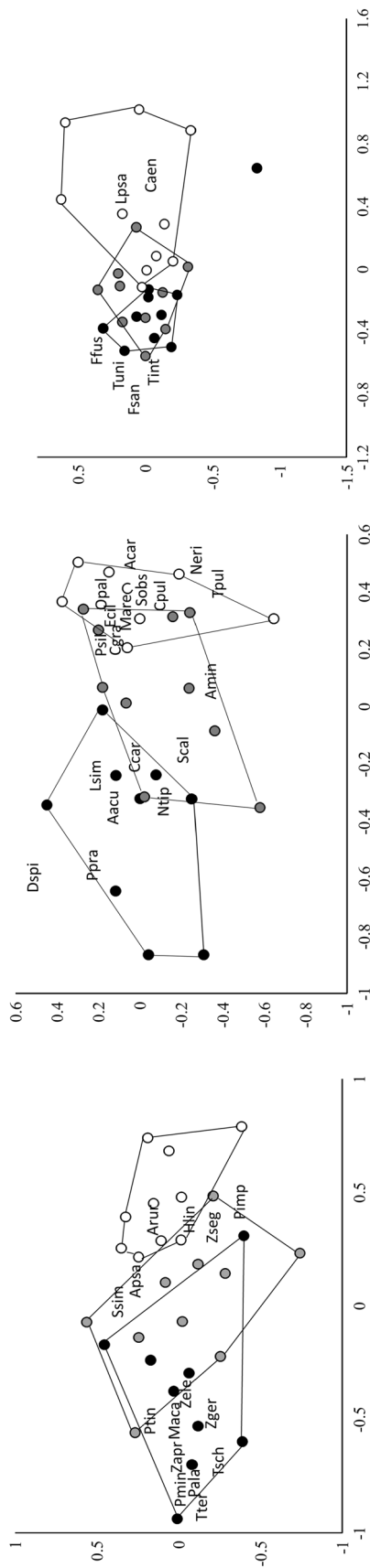


Fig. 2 NMDS ordination of sampling sites (dots) and significant indicator species for spiders (**a**), true bugs (**b**) and ants (**c**). Black dots: road verges, grey dots: forest-steppe grasslands, open circles: pastures. Species names are abbreviated with the first three letters of the genus name and the first letter of the species name (see Appendix 4 for further details)

for true bugs (19), followed by spiders (15) and ants (6) (see Appendix 4). Majority of the indicator value species of true bugs in road verges were dry grassland species (e.g., *D. spinolae*, *N. tipularis* and *Catoplatys carthusianus*), wet meadow (e.g. *L. simulans*) along with some habitat generalist species (e.g. *Palomena prasina*). Spiders were represented by xerothermic (e.g. *Z. electus*, *Z. apricorum* and *P. minimus*), habitat generalist (e.g. *T. terricola*, *Pardosa alacris* and *Zodarion germanicum*), grassland species (e.g. *M. acalypha*) and forest species (e.g. *P. tincta*). Ants population in road verges were generalist (e.g. *T. unifasciatus*), xerothermic grassland (e.g. *Temnothorax interruptus*) and dry forest species (e.g. *Formica sanguinea*).

Discussion

In this research we aimed to assess the importance of road verges in maintaining the arthropod fauna of forest-steppes. We compared species composition and FD of forest steppe grasslands and pastures with road verges. We observed higher species richness in road verges than in pastures for spiders and ants. We also found high FD values for spiders and different trait composition for all taxa in road verges when compared with forest-steppes and pastures. The characteristic species composition and the high number of indicator species for pastures and forest-steppes suggest that road verges do not serve as habitat for several grassland and forest-steppe species, in spite of the fact that numerous specialist species were found in the road verges, as well. We found that the grassland component of forest-steppes has higher species richness of spiders than pastures, and we found differences in species composition of the two habitat types for all taxa based on the multivariate analyses.

The role of road verges in maintaining arthropod biodiversity within intensively managed landscape is increasingly recognised (Schaffers et al. 2012; Reck and van der Ree 2015), as they may serve as linear habitats and dispersal corridors for weak-flying insects (Vermeulen 1994) and overwintering habitat for several specialists (Schaffers et al. 2012; Gallé et al. 2018a). In native forests, however, road verges may have a negative impact on the biota, fragmenting forest habitats by exerting barrier effects on the forest specialist species (Yamada et al. 2010). Furthermore, they may also support invasive species (Smith et al. 2007). In our study, road verges were inhabited partly by forest species from pine plantations [e.g., spiders: *P. alacris* (C. L. Koch, 1833) and *Z. germanicum* (C. L. Koch, 1837), ants: *F. sanguinea* (Latreille, 1798)]. The higher CWM shading values in road verges as compared to pastures also indicated the relatively high number of forest species. Besides forest species, we also collected open habitat generalists [e.g., spiders: *O. heterophthalmus* (Latreille, 1804), true bugs: *P. prasina*

(Linnaeus, 1761), ants: *T. interruptus* (Schenck, 1852)] and several steppe species [e.g., spiders: *Gnaphosa mongolica* (Simon, 1895), true bugs: *C. carthusianus* (Goeze, 1778)]. Thus, road verges between exotic plantations may act as secondary habitats for several specialist arthropod species. In line with these results, Koivula (2003) found that the narrow forest roadside verges are preferred by open-habitat and generalist carabid beetles.

Pine plantation forests have a relatively simple habitat structure due to the closed canopy (Gallé et al. 2014). Compared to the interior of exotic plantations, road verges between exotic forests have more open spaces, which can regulate microhabitat conditions, species composition of vascular plants and structure of the vegetation (Mullen et al. 2003; Smith et al. 2007). The dense vegetation along road verges provides high diversity of potential food for true bugs and ants, and it substantially increases the number of potential web attachment points for web-building spiders and may increase the species richness.

Moisture preference CWM values were consistently highest in road verges for all the studied taxa. This may correspond with a temperature gradient. Sandy dry pastures of the Kiskunság region often exhibit very high surface temperature during summer that can reach 60 °C (Erdős et al. 2014), and as a consequence of evaporation, there is a very low soil water content near the soil surface. These climatic parameters act as strong environmental filters (Entling et al. 2007), and as a consequence, sandy pastures have a specialized, thermophilous and xerotolerant fauna. This environmental filter reduces the diversity of trait values, resulting in low RaoQ values (Gallé et al. 2018b). Certainly, this does not imply the higher conservation value of road verges compared to grasslands and pastures.

Road verges were associated with the highest dispersal trait values for true bugs according to the linear mixed models. These narrow grassy strips in pine plantations are low quality secondary habitats for the forest-steppe fauna of true bugs, and the regular disturbance may preclude the effective colonization of several wingless species. Dispersal ability clearly influences the colonization of true bugs (Moir et al. 2005), resulting in higher dispersal trait values of true bugs in more disturbed habitats (Torma et al. 2019). Well-dispersing species with developed wings can travel long distances (presumably several kilometres, see Kiritani and Sasaba 1969), but they probably travel as far as necessary to locate the nearest host plant or suitable habitat patch (Tillman et al. 2009). The type of vegetation and land use primarily affects the species composition and richness of true bug assemblages (Zurbrugg and Frank 2006; Torma and Császár 2013; Torma et al. 2017), thus, besides dispersal limitation, specialized habitat requirements of species and the density of potential host plants may be the most important determinants of colonization pattern of true bugs in road verges.

Conclusion

Our study emphasizes the importance of road verges in exotic plantations for the conservation of arthropod diversity. With the change of natural habitats to exotic or semi-natural forests, it is important to maintain every aspect of this grassland habitat that has the capability to protect this unique biodiversity. Our results indicate that road verges should be considered an important reserve for grassland specialists, as they provide secondary linear habitats for many arthropod species. Road verges are often maintained by forestry management, and this disturbance may reduce their conservation capabilities. We suggest the maintenance of these grassy strips in order to preserve arthropod biodiversity.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval The study did not involve endangered or protected species and we did not collect arthropods in protected areas.

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